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Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk

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Males may increase their fitness through extra-pair copulations (copulations outside the pair bond) that result in extra-pair fertilizations, but also risk lost paternity when they leave their own mate unguarded. The fitness costs of cuckoldry for Seychelles warblers (*Acrocephalus sechellensis*) are considerable because warblers have a single-egg clutch and, given the short breeding season, no time for a successful replacement clutch. Neighbouring males are the primary threat to a male's genetic paternity. Males minimize their loss of paternity by guarding their mates to prevent them from having extra-pair copulations during their fertile period. Here, I provide experimental evidence that mate-guarding behaviour is energetically costly and that the expression of this trade-off is adjusted to paternity risk (local male density). Free-living males that were induced to reduce mate guarding spent significantly more time foraging and gained significantly better body condition than control males. The larger the reduction in mate guarding, the more pronounced was the increase in foraging and body condition (accounting for food availability). An experimental increase in paternity risk resulted in an increase in mate-guarding intensity and a decrease in foraging and body condition, and vice versa. This is examined using both cross-sectional and longitudinal data. This study on the Seychelles warbler offers experimental evidence that mate guarding is energetically costly and adjusted to paternity risk.

Keywords: extra-pair copulation; paternity risk; mate guarding; foraging; body condition; reproductive success

1. INTRODUCTION

In many monogamous avian species males increase their reproductive success by adopting a mixed strategy whereby they seek extra-pair copulations (copulations with females other than their social mate) and guard their fertile mates to prevent them from copulating with other males (Trivers 1972; Birkhead & Møller 1992). Extra-pair copulations resulting in extra-pair fertilizations are widespread in birds (e.g. Birkhead *et al.* 1990; Gibbs *et al.* 1990; Birkhead & Møller 1992; Kempenaers *et al.* 1992; Dixon *et al.* 1994; Wetton *et al.* 1995). The most common anti-cuckoldry tactic used by males is mate guarding (Birkhead & Møller 1992). Mate guarding involves the close following of females by their mates during the female's fertile period (starting several days before the onset of egg laying and lasting until clutch completion), enabling the pair male to interfere with would-be cuckolders (Beecher & Beecher 1979; Birkhead 1979). Although mate guarding is known to reduce extra-pair copulations, it should impose costs on males that translate into increased energy expenditure (e.g. due to an increase in vigilance and deterrence activities, or constraints on foraging) and reduced pursuit of extra-pair copulations on their own account (see Hohman 1986; Birkhead *et al.* 1987; Sherman & Morton 1988; Andersson 1994; Westneat 1994; Alberts *et al.* 1996). This might well be a reason why mate-guarding intensity is adjusted to the risk of extra-pair paternity, i.e. intrusion pressure from extra-pair males, and female extra-pair behaviour (e.g. Alatalo *et al.* 1987; Møller 1987; Hanski 1994; Gray 1996). Some genetic studies have shown that the risk of paternity is affected by a variety of factors, including breeding density and operational sex ratio (Gibbs *et al.* 1990; Westneat *et al.* 1990; Gowaty & Bridges 1991; Birkhead & Møller 1992; Møller & Birkhead 1993; Hasselquist *et al.* 1995). In this study on the Seychelles warbler (*Acrocephalus sechellensis*) I test experimentally whether mate guarding is energetically costly and whether paternity risk affects the time allocated to mate guarding and to foraging in males. Despite their critical importance for testing sexual-selection models, these costs have not been examined before (see also Hixon 1987; Partridge & Endler 1987; Askenmo *et al.* 1992; Andersson 1994; Arnqvist 1994; Watson & Lighton 1994; Alberts *et al.* 1996; Sparkes *et al.* 1996).

The entire world population of Seychelles warblers is confined to three islands: Cousin (29 ha), Cousine (26 ha) and Aride (68 ha). A salient advantage of field experiments with this species is that every single adult bird is individually recognizable by means of unique leg-ring combinations. Breeding density differs between islands (Komdeur & Kats 1999). Once paired, the breeding pair remains together in the same territory until the death of one member of the pair (Komdeur 1991). The level of extra-pair fertilizations is high (41.8%, $n = 55$ broods; Richardson *et al.* 2001). The fitness costs of cuckoldry are considerable because warblers usually have clutches of a single egg, are single brooded with restricted breeding seasons and have no time for a successful replacement clutch (Komdeur 1996*a*), and both sexes feed the young equally during the four-month period of dependence (Komdeur 1991). Neighbouring reproductive males are the primary threat to a male's genetic paternity: 85% of extra-pair copulations ($n = 20$) involve neighbouring males (Komdeur *et al.* 1999) and 73.9% of extra-pair young ($n = 23$) are sired by neighbouring males (Richardson *et al.* 2001). To minimize paternity loss, males guard their females only during the fertile period (from 6 days before until the day of egg laying). In the

Seychelles warbler the male abruptly ceases mate guarding the moment he spots a single-egg clutch in the nest. By introducing a model egg into the nest during the female's fertile period before egg laying, the male can be induced to stop mate guarding. Consequently, the rate of intrusions by other males and the rate of successful extra-pair copulations are significantly higher than those observed in control groups, and the frequency of successful extra-pair copulations increases significantly with number of neighbouring adult males (Komdeur *et al.* 1999). Although Seychelles warblers often breed cooperatively, in this study I used only pairs without helpers.

This study was designed to answer three questions. First, is mate guarding energetically costly? In other words, is an increase in the time allocated to mate guarding associated with a reduction in body condition? Second, if mate guarding incurs an energetic deficit, is this a consequence of reduced foraging activity during the mate-guarding phase? I investigate this trade-off experimentally by inducing some males to stop mate guarding. If mate guarding is costly, I expect males to increase foraging and body condition after a reduction in mate guarding. This manipulation allowed me to compare the differences in foraging time and body condition of experimental and control males before and after manipulation. Third, is an increased cuckoldry risk associated with a higher mate-guarding intensity and lower foraging activity and body condition? I test this through experimental changes to paternity risk.

2. MATERIAL AND METHODS

(a) *Study population and watches of focal pairs*

The Seychelles warblers were studied between June and September (the main breeding period) on Cousin Island in 1990, 1996 and 1997, and on the islands of Cousine and Aride in 1996 and 1997. All adult birds present on the islands were individually colour marked and were of known age and sex. To quantify mate-guarding behaviour, we observed a total of 40 different breeding pairs on Cousin, 13 different pairs on Cousine and nine different pairs on Aride in 1996 and 1997. To control for potential effects of age (Welling *et al.* 1995) and breeding experience (Kempenaers *et al.* 1995), the focal pairs consisted of warblers aged between 3 and 6 years (an interval during which there are no age effects on mate guarding and foraging; Komdeur 1996*b*) that had all successfully produced a fledgling before the onset of the study. All territories were checked weekly for initiation of nest building by following females for 30 min (Komdeur 1991). During the nest-building period, which lasts up to 19 days (Komdeur 1991), nests were checked daily for the presence of an egg (at inaccessible sites this was done using a mirror attached to a stick). In this study the clutch size of all pairs was one egg. Focal-pair watches were conducted daily during the female's fertile period (starting 4–5 days before egg laying and lasting until the day of egg laying). The warblers are remarkably tame and easily observed. Every day, between 30 min after sunrise and 10.00 the male and female of each pair were observed simultaneously and continuously for 30 min; one observer watched the female and another simultaneously kept track of the male. It was decided who would observe the male and the female by tossing a coin. For each pair I precisely determined the quality of the territory they inhabited (see § 2c) and the local male density, expressed as the number of reproductive males (aged over 8 months; Komdeur 1996*b*) present in adjacent territories during the entire observation period. When both members of the pair were located the following measures were recorded.

(i) *Male foraging behaviour*

I recorded whether or not the male was foraging (swallowing food) during 30 s intervals. Percentage foraging was expressed as the percentage of the total time-blocks during which the warbler ingested at least one prey item.

(ii) *Distances between pair members and birds from other territories*

Distances between pair members were recorded as less than or greater than 5 m at 30 s intervals. The distance of 5 m was chosen because this is the maximum distance at which both warblers can be kept in view. If the distance was less than 5 m then the birds' identities were recorded. The proximity of the male to the female was analysed as the proportion of observations where the male and female were within 5 m of each other when the female was off the nest. I took the proximity of the male to the female as a measure of mate-guarding behaviour because proximity was positively correlated with the percentage of mate following by the male ($r^2 = 0.66$, $n = 40$, $p < 0.001$; see also Komdeur *et al.* 1999). None of the extra-pair-copulation attempts or successful extra-pair copulations occurred when the male was within 5 m of his mate. An experimental increase in the distance between the male and his mate during the fertile period resulted in significantly more extra-pair copulations by the female (Komdeur *et al.* 1999).

(iii) *Attempted and successful copulations*

A copulation attempt was defined as a male trying to mount a female from above, and a successful copulation was defined as a copulation where the female allowed the male to mount for a few seconds (see also Arvidsson 1992).

(iv) *Territorial or aggressive incidents between the pair male, the pair female and intruding birds*

When territorial or aggressive incidents between the pair male, the pair female and intruding birds occurred, the intruding bird's identity was recorded whenever possible.

(b) *Trade-off experiments*

(i) *Experimentally terminated mate guarding*

In 1996 and 1997 I tested whether mate guarding is energetically costly. I induced some males to cease mate guarding by placing a model Seychelles-warbler egg in the empty nest when the female was lining the nest (1–4 days before the first egg was laid) (Komdeur *et al.* 1999). The model eggs were made of wax and painted with a waterproof marker to match the pattern of real warbler eggs. Models were placed during the early morning to mimic the laying time of real eggs, and the presence or absence of the model egg and real egg were checked daily during the observation period. The model-egg experiments were successfully conducted on 20 pairs, i.e. model eggs were 'laid' within the female's fertile period and females laid an egg in the nest containing the model egg. In these experiments, a real egg was laid 1 ($n = 2$), 2 ($n = 4$), 3 ($n = 8$) or 4 ($n = 6$) days after the addition of the model egg. I observed females and males on the day before adding the model egg and on the days between adding the model egg and the laying of the real egg, using the protocol described in § 2a. As a control, I performed the same actions around the nests of 20 pairs, but without adding a model

egg. On the day before the experimental reduction in mate guarding, nine experimental and seven control males were trapped to take measurements of mass and tarsus length. Body mass was measured to the nearest 0.1 g using a 50 g Pesola balance (Pesola AG, Baar, Switzerland), and tarsus length was measured to the nearest 0.1 mm using vernier callipers. To evaluate the energetic costs of mate guarding and to check for possible changes in male body condition over time, these males were caught and measured at three other times: 30–25 days and 18–15 days before the laying of a real egg by their mate (no mate guarding; Komdeur *et al.* 1999) and 1–2 days after the experimental reduction in mate guarding.

(ii) *Experimental removals and translocations*

To test whether a change in paternity risk contributes to changes in mate guarding and foraging I conducted two experiments. First, on Cousin Island nine focal pairs were selected with four ($n = 4$), five ($n = 2$) or six ($n = 3$) reproductive males in neighbouring territories. During the female's fertile period (2–3 days before egg laying), I removed 17 reproductive males from the surrounding territories, such that all focal pairs were left with three neighbouring reproductive males. The territories chosen for removals were separated from each other by at least four territories to avoid mutual interactions, and all removals at one focal site were conducted on the same day. The experiment was conducted between 29 June and 1 July 1990, and the removed males were transferred to Cousine Island. During the same period three control pairs (with the female in the fertile period) were selected, each with three neighbouring reproductive males that were not manipulated. The focal males were observed daily for a 30 min period on the 2 days before the removal and on the 2 days after the removal but before egg laying (using the protocol described in § 2a). Second, the transfers of warblers from Cousin to Cousine (1990) and from Cousin to Aride (1988) and the subsequent population increase on Cousine and Aride resulted in significantly lower and higher, respectively, local male densities than on Cousin in 1996 and 1997. This allowed me to test whether the paternity risk in the new habitat affects mate guarding and foraging intensity.

(c) *Territory quality*

Seychelles warblers are insectivorous, and so territory quality was expressed as the mean number of prey invertebrates available in a territory (for methods, see Komdeur 1991, 1994), which was positively correlated with adult survival and reproductive success (Komdeur 1991). The qualities of all territories on Cousin, Cousine and Aride were assessed monthly during the study period.

(d) *Data analyses*

Focal-pair observations in 1990, 1996 and 1997 involved different pairs to avoid duplications. Observations were related to the laying of the first egg (day 0). For each variable I calculated a mean daily value across all pairs from day −4 to day 0. To determine a trade-off between mate guarding and foraging, I assigned each experimental pair to a control pair, such that both pairs were observed in the same week and on the same two consecutive days before day 0 (comprising the day before and the day of adding the model egg to the nest of the experimental pair). I calculated the change in mate guarding as the amount of mate guarding observed on the day the model egg was 'laid' minus the amount of mate guarding observed on the previous day. The change in foraging is expressed in a similar way. To calculate a male-body-condition index I used the residuals derived from the regression of tarsus length on body mass (*cf.* Packard & Boardman 1987). To ensure that the residuals reflected possible energetic costs of mate guarding, the regression line was determined using measurements of body mass and tarsi from 48 males that, at the time of capture, were not involved in breeding activity (mass = 1.81 × tarsus − 32.79, $r^2 = 0.75$, $n = 48$, $p < 0.001$). For experimental and control males captured twice between day −4 and day 0, I calculated the change in body condition as the body mass measured on the recapture day minus the mass measured on the day the model egg was 'laid'.

Most variables deviated from normality, so I used non-parametric statistics for most of the analyses. All parametric analyses were based on arcsine–square-root transformed data. Unless stated otherwise, means are expressed as mean ± s.e.m., probability values are two-tailed and the null hypothesis was rejected at $p < 0.05$.

3. RESULTS

(a) *Trade-offs between mate guarding, foraging and body condition*

There is evidence for a trade-off between mate guarding and foraging by the male. The more time the male spent mate guarding the less he spent foraging (figure 1*a*). The average times spent foraging and mate guarding by experimental males the day before the introduction of the model egg (and the induced reduction in mate guarding) were similar to those of control males in the corresponding period (mean mate guarding: 53.0 ± 4.9% versus 50.3 ± 3.9%, Wilcoxon paired-sample test $Z = 0.604$, $n = 20$, $p = 0.546$; mean foraging: 69.9 ± 4.5% versus 70.0 ± 4.2%, $Z = 0.644$, $n = 20$, $p = 0.519$ for the experimental and control males, respectively; figure 1*a*). In addition, there was a negative correlation between the amount of mate guarding and body condition (figure 1*b*). The average body conditions of experimental and control males were similar (mean body condition: −0.14 ± 0.29 g, $n = 9$ versus 0.14 ± 0.11 g, $n = 7$ for experimental and control males, respectively). The amount of mate guarding and foraging, and the body condition, were independent of the amount of food present in the territory (mate guarding: $r^2 = 0.01$, $n = 40$, $p = 0.606$; foraging: $r^2 = 0.05$, $n = 40$, $p = 0.165$; body condition: $r^2 = 0.01$, $n = 16$, $p = 0.774$). The male's body condition had no effect on the probability of successfully expelling an intruding male from his territory (*G*-test of independence: $D = 2.12$, d.f. = 1, $n = 16$, $p = 0.145$).

If there is an energetic cost of mate guarding due to lowered foraging activity, I would expect that after an experimental reduction in mate guarding, males would spend more time foraging and, hence, gain a better body condition. In addition, the changes in foraging time and body condition of experimental males over the experimental period should be greater than those of control males over the same period. Immediately after adding the model eggs to the warbler's nests (on the same day), the experimental males spent less time mate guarding than the control males (15.6 ± 5.5% versus 54.1 ± 21.2%, respectively, $Z = 3.921$, $n = 20$, $p < 0.001$; see also Komdeur *et al.* 1999). The experimental males also spent less time mate guarding on the day the model egg was added than they had the day before (15.6 ± 5.5% versus

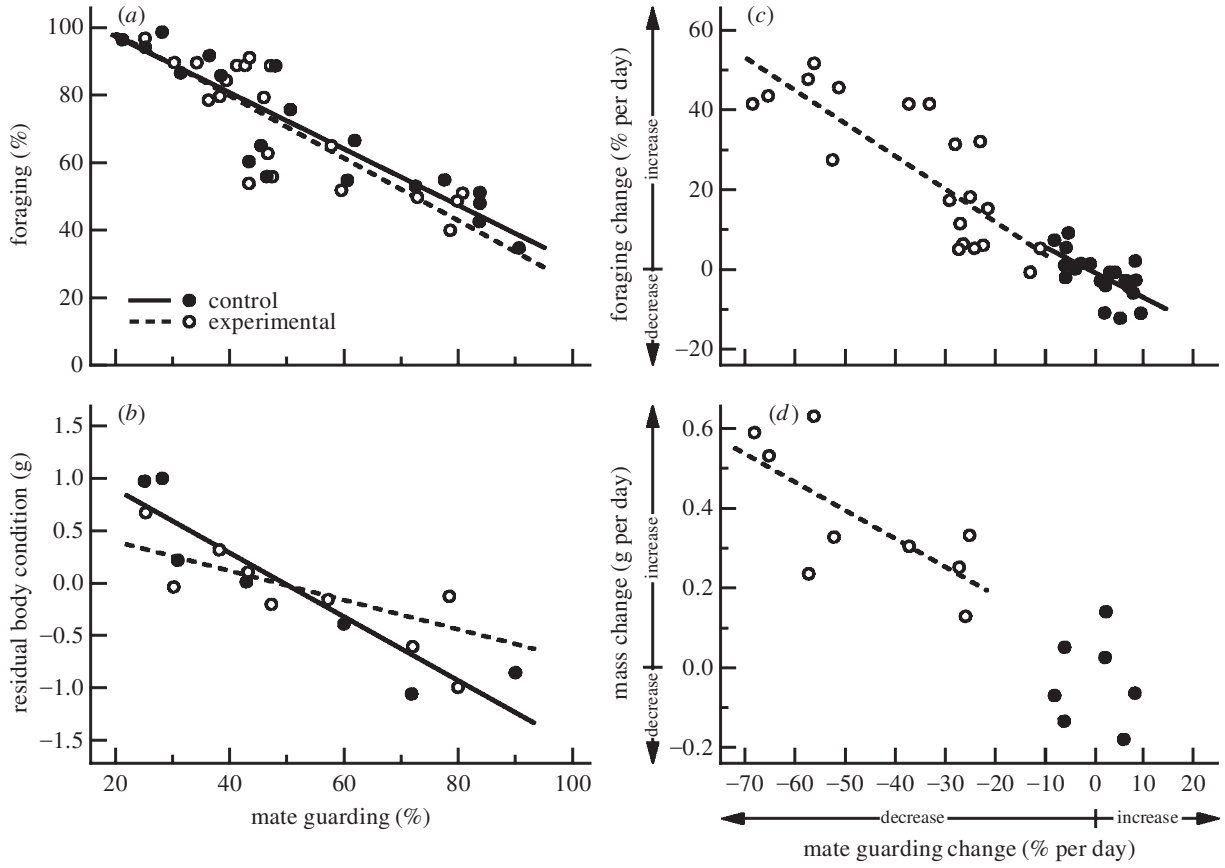

Figure 1. (*a*) The influence of the percentage of time spent mate guarding (*x*-axis) on the percentage of time spent foraging (*y*-axis) by male Seychelles warblers during days 4 and 3 before egg laying (control: $y = -0.84x + 114.58$, $r^2 = 0.81$, $n = 20$, $p < 0.001$; experimental: $y = -0.93x + 116.60$, $r^2 = 0.74$, $n = 20$, $p < 0.001$). (*b*) The influence of the percentage of time spent mate guarding (*x*-axis) on the residual body condition (*y*-axis) during days 4 and 3 before egg laying (control: $y = -0.02x + 1.47$, $r^2 = 0.85$, $n = 7$, $p = 0.003$; experimental: $y = -0.01x + 0.84$, $r^2 = 0.65$, $n = 9$, $p = 0.009$). (*c*) The influence of the change in the percentage of time spent mate guarding (*x*-axis) on the change in the percentage of time spent foraging (*y*-axis) within individuals (observations on the day of 'laying' the model egg minus observations on the previous day) (control: $y = -0.64x + 0.10$, $r^2 = 0.41$, $n = 20$, $p = 0.002$; experimental: $y = -0.82x + 4.14$, $r^2 = 0.65$, $n = 20$, $p < 0.001$). (*d*) The influence of the change in the percentage of time spent mate guarding (*x*-axis) on the change in body mass (*y*-axis) within individuals (change in body mass = (body mass on recapture day − body mass on the day the model egg was 'laid' in the nest)/number of days between capture and recapture) (control: $r^2 = 0.005$, $n = 7$, $p = 0.885$; experimental: $y = -0.007x + 0.048$, $r^2 = 0.51$, $n = 9$, $p = 0.031$). All observations and the experimental reductions of mate guarding took place 4–1 days before a real egg was laid in the nest. Observations were conducted in 1996 and 1997.

50.3 ± 17.3%, $Z = 3.920$, $n = 20$, $p < 0.001$), whereas control males spent similar amounts of time mate guarding on both days (54.1 ± 21.2% versus 53.0 ± 21.7% on the second and first days, respectively; $Z = 0.898$, $n = 20$, $p = 0.369$). The change in the amount of mate guarding on the day the model egg was introduced compared with that on the day before was significantly higher for experimental males than for control males (−34.7 ± 3.8% versus 1.1 ± 1.2%, $Z = 3.921$, $n = 20$, $p < 0.001$; figure 1*c*). The larger the experimental reduction in mate guarding, the more pronounced was the increase in foraging time (figure 1*c*). Experimental males spent more time foraging on the day the model egg was added than they had the day before (94.3 ± 2.3% versus 70.0 ± 18.6%, $Z = 3.886$, $n = 20$, $p < 0.001$), whereas control males spent similar amounts of time foraging on both days (68.2 ± 18.7% versus 69.9 ± 20.3% for the first and second days, respectively, $Z = 1.412$, $n = 20$, $p < 0.158$). The increase in the amount of foraging on the day the model egg was introduced compared with the day before was significantly higher for experimental males than for control males (24.3 ± 3.9% versus −1.7 ± 1.2%, $Z = 3.716$, $n = 20$, $p < 0.001$; figure 1*c*).

The average body masses of males that were caught and recaptured during two periods when they were not involved in mate guarding (30–25 days and 18–15 days, respectively, before the laying of a real egg by the female) were similar to the average mass of the same males recaptured at the onset of the mate-guarding period (4–2 days before the laying of a real egg by the female) (15.8 ± 0.3 g at 30–25 days, 16.1 ± 0.3 g at 18–15 days and 16.0 ± 0.3 g at 4–2 days, $n = 16$, MANOVA (repeated measures), $F = 1.062$, d.f. = 2, $p = 0.372$). The initial body masses of experimental and control males on the day the egg was added were similar (16.0 ± 0.3 g ($n = 9$) for experimental males versus 16.1 ± 0.2 g ($n = 7$) for control males). After adding the model egg the experimental males gained significantly in body mass. The larger the reduction in mate guarding of the experimental males, the more pronounced was the increase in

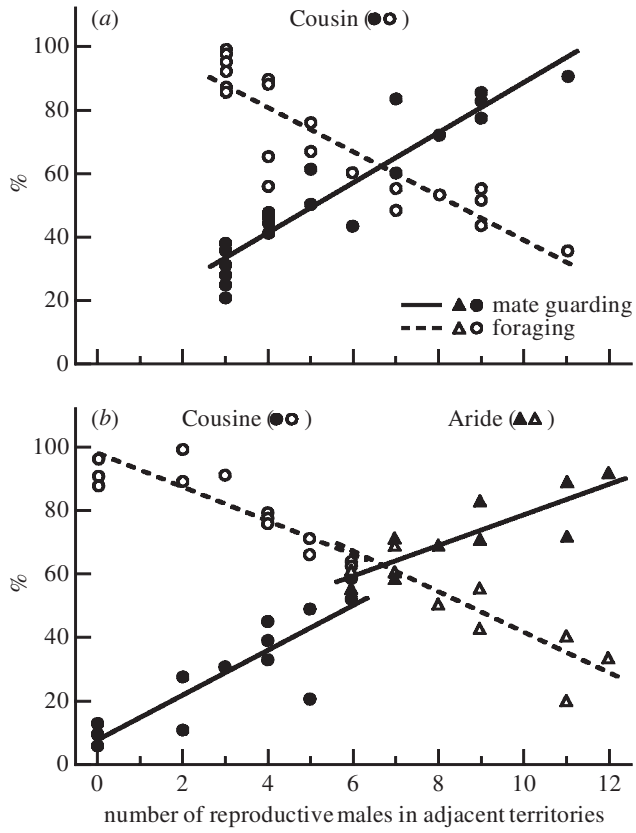

Figure 2. The influences of the number of neighbouring reproductive Seychelles warbler males (*x*-axis) on the percentages of time spent mate guarding and foraging (*y*-axis) by male Seychelles warblers during days 2 and 1 before egg laying on (*a*) Cousin Island and (*b*) the islands of Cousine and Aride (Cousin, mate guarding: $y = 7.49x + 12.93$, $r^2 = 0.71$, $n = 20$, $p < 0.001$; Cousin, foraging: $y = -7.03x + 108.56$, $r^2 = 0.79$, $n = 20$, $p < 0.001$; Cousine, mate guarding: $y = 7.83x + 4.59$, $r^2 = 0.68$, $n = 13$, $p < 0.001$; Cousine, foraging: $y = -5.38x + 96.66$, $r^2 = 0.81$, $n = 13$, $p < 0.001$; Aride, mate guarding: $y = 4.91x + 29.60$, $r^2 = 0.73$, $n = 9$, $p = 0.004$; Aride, foraging: $y = -6.29x + 103.47$, $r^2 = 0.747$, $n = 9$, $p = 0.003$). For the focal territories the mean number of reproductive males in adjacent territories and mean of the proximity of males to their mates were significantly higher on Aride than on Cousine (mean number of adjacent males: Aride mean ± s.e.m. = 8.9 ± 2.1, Cousine mean ± s.e.m. = 3.9 ± 1.7, $U = 3.87$, $p < 0.001$; mean mate guarding: Aride mean ± s.e.m. = 73.0 ± 4.0%, Cousine mean ± s.e.m. = 35.4 ± 5.1%, $U = 3.84$, $p < 0.001$). Observations were conducted in 1996 and 1997.

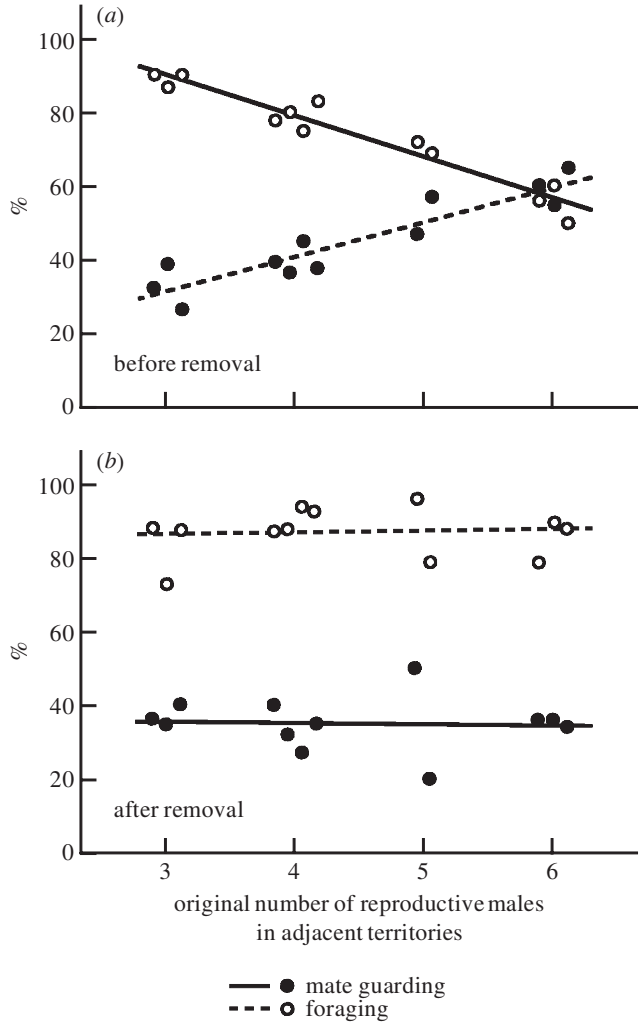

Figure 3. The influences of the number of neighbouring reproductive Seychelles warbler males (*x*-axis) on the percentages of time spent mate guarding and foraging (*y*-axis) by male Seychelles warblers during the pair female's fertile period on Cousin Island, (*a*) before the removal of neighbouring males at 4–3 days before egg laying (mate guarding: $y = 9.30x + 4.17$, $r^2 = 0.85$, $n = 12$, $p < 0.001$; foraging: $y = -11.05x + 122.97$, $r^2 = 0.94$, $n = 12$, $p < 0.001$) and (*b*) after the removal of neighbouring males at 2–1 days before egg laying, through which the number of neighbouring males was reduced to three for all pairs (mate guarding: $r^2 = 0.002$, $n = 12$, $p = 0.883$; foraging: $r^2 = 0.004$, $n = 12$, $p = 0.847$). Observations were conducted in 1990.

body mass (figure 1*d*). The daily increase in body mass was significantly associated with the increase in foraging activity ($r^2 = 0.65$, $n = 16$, $p < 0.001$). One day after adding the model egg, the mass of recaptured males had increased by 0.4 g (mass on the day of egg addition = 15.9 ± 0.3 g, mass 1 day after egg addition = 16.3 ± 0.19 g ($n = 5$)). Two days after adding the model egg, the mass of recaptured males had increased by 0.9 g (mass on the day of egg addition = 15.9 ± 0.2 g, mass 2 days after egg addition = 16.8 ± 0.2 g ($n = 4$)). The average daily increase in body mass per individual male was 0.42 g ((5(0.4 g/1 day) + 4(0.9 g/2 days))/9). In contrast, the masses of recaptured control males remained the same during the corresponding period (mass on the day of egg addition = 16.1 ± 0.3 g, mass 1 day after egg addition = 16.1 ± 0.2 g ($n = 4$); mass on the day of egg addition = 16.0 ± 0.3 g, mass 2 days after egg addition = 15.8 ± 0.4 g ($n = 3$)). Given a significant effect of the interaction between recapture day and treatment on the change in body mass (recapture day treatment: $F_{1,15} = 18.26$, $p = 0.010$), there is a significant effect of both day and treatment. However, for each treatment the effect of recapture day was different (treatment: $F_{1,15} = 39.82$, $p < 0.001$; day of recapture: $F_{1,15} = 1.54$, $p = 0.238$). The average mass of a male caught 0–4 days before the onset of mate guarding was 16.2 ± 0.8 g ($n = 48$). On average, a mate-guarding male looses 0.42 g per day. Given that intense mate guarding lasts for a minimum of 5 days (Komdeur *et al.* 1999), the total mass loss during a 5 day mate-guarding period is

estimated to be 2.1 g, which corresponds to 13.0% of the initial body mass.

(b) *Paternity risk and mate guarding*

On Cousin Island the average time spent mate-guarding during the 2 days before egg laying increased significantly with the number of neighbouring reproductive males (figure 2*a*). The amount of food present in the focal territories had no effect on mate guarding (Cousin: $r^2 = 0.04$, $n = 20$, $p = 0.380$; Aride: $r^2 = 0.19$, $n = 9$, $p = 0.245$; Cousine: $r^2 = 0.14$, $n = 13$, $p = 0.210$). The transfers of warblers from Cousin to Cousine and from Cousin to Aride confirmed the dependency of mate-guarding behaviour on local male density. The mean number of neighbouring reproductive males per focal territory on Aride was 2.3 times higher than on Cousine (figure 2*b*). Males on Aride displayed a significantly higher mate-guarding intensity than males on Cousine (figure 2*b*). The mean values of mate guarding recorded on Aride and Cousine were similar to those on Cousin when corresponding numbers of reproductive males were present in adjacent territories (figure 2).

(c) *Paternity risk and trade-off between mate guarding and foraging*

Mate guarding and foraging behaviour during the fertile period of the female was, indeed, adjusted to local male density. The higher the number of reproductive males present in adjacent territories, the more time was spent mate guarding and the less time was spent foraging by the focal male (figure 3*a*). However, immediately after reducing the number of neighbouring males to three for all focal pairs, mate-guarding time decreased significantly and foraging time increased significantly (figure 3*b*). The more neighbouring males were removed, the more pronounced were both the subsequent decrease in mate guarding and the subsequent increase in foraging times. However, there were no changes in the mate-guarding and foraging behaviours of the control males during the corresponding periods (figure 3*a*,*b*). After the removal experiment, the amount of time spent mate guarding and foraging by the experimental males became similar to that of the control males (both categories with three neighbouring males, figure 3*b*).

4. DISCUSSION

(a) *Trade-off of mate guarding*

Parents should optimize the parental-investment mechanisms by which they can maximize their lifetime reproductive success. It is argued that guarding their mates against extra-pair copulations is an important form of indirect male investment in several species. Theory suggests that males should invest heavily in mate guarding if the female can be fertilized only during a brief predictable period (e.g. Parker 1974; Ridley 1983), if there is a high paternity risk (e.g. Alatalo *et al.* 1987; Birkhead & Biggins 1987; Møller 1987; Westneat *et al.* 1990; Meek & Robertson 1994; Iribarne *et al.* 1995; Slagsvold & Lifjeld 1997) and if males invest heavily in paternal care (Westneat 1988; Van Rhijn 1991; Westneat & Sherman 1993). The Seychelles warbler obeys these criteria: it is single-brooded with an annually predictable short period (1 month) during which egg laying takes place (Komdeur 1996*a*); the rate of extra-pair paternity (Richardson *et al.* 2001) is very high compared with other avian species (Cockburn 1998; Lundy *et al.* 1998) and both sexes feed the single young equally during the 4 month period of dependence (Komdeur 1991). Male warblers display an efficient form of mate guarding over time: only during the fertile period do males guard and defend their mates aggressively from males attempting extra-pair copulations; during the pre-fertile period and the period after the egg is laid males do not guard their mates (Komdeur *et al.* 1999). Although theoretical analyses explicitly assume that there are energetic costs of optimal male time-investment strategies (Andersson 1994), empirical and experimental evidence for this was hitherto non-existent (Partridge & Endler 1987; Arnqvist 1994; Watson & Lighton 1994). Empirical evidence for a trade-off between mate guarding and foraging comes from only three studies, which demonstrated that males increase their mate-guarding time when they are better nourished (the blackbird, *Turdus merula* (Cuthill & MacDonald 1990); the baboon, *Papio cynocephalus* (Alberts *et al.* 1996); and the blue milkweed beetle, *Chrysochus cobaltinus* (Dickinson 1995)). Supportive evidence for the energetic consequences of mate guarding comes from only one study (in rock pipits, *Anthus spinoletta*), where an observed decrease in foraging and an increase in weight loss of males close to laying was suggested as a means of allocating more time to mate guarding (Askenmo *et al.* 1992). It is argued that if mate guarding is energetically costly, males should reduce mate-guarding time and increase foraging time when their mates have laid their last eggs (Askenmo *et al.* 1992; Hanski 1994).

The Seychelles warbler is the first species to offer an experimental demonstration and quantification of a trade-off between mate guarding and foraging in males, and of the energetic deficits entailed by mate guarding. First, the more time spent mate guarding, the less time is spent foraging and the lower is the body condition. Second, experiments have demonstrated that mate guarding stops completely after the laying of a single egg (the entire clutch) (Komdeur *et al.* 1999). Third, free-living males that were induced to reduce mate guarding spent significantly more time foraging and gained significantly more body mass than males in the control group. Fourth, within-male comparisons showed that the larger the reduction of mate guarding in the experimental group, the larger was the increase in foraging and the more pronounced was the increase in body condition. The observed decrease in male condition with increasing time spent mate guarding could also be attributed to the existence of a trade-off between the time spent foraging and the time spent courtship-feeding their mates (Davis & Graham 1991), whereas the increase in condition after mate guarding stops may reflect preparation for the energetic demands of incubation (Mertens 1980; Yom-Tov & Hilborn 1981; Williams 1991, 1996; Siikamaki 1995). However, this is not the case in the Seychelles warbler because males do not feed their partners during courtship (Komdeur 1991) and do not incubate the clutch (Komdeur 1996*b*). Although not measured in this study, the energetic deficits entailed by mate guarding could also be attributed to the actual energetic costs of mate

guarding (i.e. flying greater distances, chasing away intruders and defending the female from harassment and extra-pair copulation attempts). However, reductions in foraging and body mass are not necessarily costs of mate guarding but could also be consequences of an optimal allocation or an adaptive response to improved aerial performance when chasing intruders (Calder *et al.* 1990; Norberg 1990). There is good evidence that this is not true for the Seychelles warbler: males do not increase in body mass before the onset of the mate-guarding period and the chance of successfully expelling an intruding male, which involves chases lasting up to 10 s, is independent of male body mass. Given the energetic consequences of mate guarding, the condition of the male may limit the reserves that he can spend on mate guarding. For example, in the barn swallow (*Hirundo rustica*) male body mass is positively associated with the time spent mate guarding (Møller 1987). Heavier males are probably less often cuckolded, because they can perform longer and more intense mate guarding. For the Seychelles warbler, mate guarding is a substantial investment. The minimum known survival mass for males is 13.8 g (Komdeur 1997), which is only 0.3 g below the estimated mass of 14.1 g (16.2 g–2.1 g) on the last day of the mate-guarding period. However, the energy losses were recouped rapidly after the male had ceased mate guarding.

Apart from the energetic deficit incurred through mate guarding, mate guarding in many socially monogamous species is both time consuming and largely incompatible with pursuing extra-pair copulations (Carlson *et al.* 1985; Møller 1985; Alatalo *et al.* 1987; Brodsky 1988; Hasselquist & Bensch 1991; Van Rhijn 1991, but see Birkhead & Møller 1992). When the egg-laying period of the pair female ends, the male is released from these constraints and can devote more time to pursuing extra-pair copulations. In the Seychelles warbler, males do not incubate, and for most males in this study the opportunities for extra-pair copulations during the incubation period remained high (J. Komdeur, unpublished data). To date, few studies have examined the relationship, within individual males, between the amount of mate guarding and the number of extra-pair fertilizations obtained, incorporating genetic analysis of paternity.

(b) *Paternity risk and trade-off between mate guarding and foraging*

It is argued that, if mate guarding incurs an energetic deficit, males should reduce mate-guarding time and increase foraging time with decreasing risk of cuckoldry (Askenmo *et al.* 1992; Hanski 1994). This paper adduces evidence to test this idea. First, males adjusted the trade-off in response to short-term changes in the perceived risk of cuckoldry. An experimental reduction in the cuckoldry risk during the fertile period of the female resulted in a decrease in mate guarding and an increase in foraging activity. Second, the transfers of breeding pairs from Cousin to Cousine with low, and to Aride with high, numbers of reproductive males in adjacent territories showed that males increased mate guarding and decreased foraging with increasing likelihood of being cuckolded. Although the food densities on Cousine and Aride were significantly higher than on Cousin (Komdeur 1996*a*), male warblers on the new islands did not increase foraging time while mate guarding: the amount of foraging was similar to that on Cousin after controlling for paternity risk. Thus, this study reveals that on a proximate basis the expression of the trade-off between mate guarding and foraging is not adjusted to the availability of food within a territory but to the male's risk of being cuckolded. This study clearly demonstrates that mate-guarding behaviour is energetically costly and that the expression of this trade-off is adjusted to paternity risk, and I expect that, given the theoretical models predicting energetic costs of optimal time-investment strategies, these findings are representative of other animal taxa.

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